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RESEARCH ARTICLE

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# Within-year and among-year variation in impacts of targeted conservation management on juvenile survival in a threatened population

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## Abstract

1. Overall impacts of targeted conservation interventions on population growth rate ($\lambda$) will depend on within-year and among-year variation in exposure of target individuals to interventions, and in intervention efficacy in increasing vital rates of exposed individuals. Juvenile survival is one key vital rate that commonly varies substantially within and among years, and consequently drives variation in $\lambda$. However, within-year, among-year and overall impacts of targeted interventions on population-wide survival probabilities of potentially mobile juveniles are rarely quantified, precluding full evaluation and evidence-based refinement of interventions.
2. We applied multi-state mark–recapture models to 8 years of ring–resighting data from a threatened red-billed chough *Pyrrhocorax pyrrhocorax* population to quantify within-year and among-year variation in juvenile exposure to a targeted intervention of supplementary feeding and parasite treatment, and to estimate efficacy in increasing juvenile survival probability. We then combined and up-scaled these estimated effects to evaluate the impact of the 8-year intervention on overall population-wide survival probability and resulting population size.
3. High proportions of surviving juveniles (>70%) were exposed to the intervention across the annual biological cycle in all years. Exposure was associated with higher short-term survival probabilities through the full annual cycle. Consequently, management increased estimated population-wide annual juvenile survival by approximately 0.14. However, such effects were only evident in cohorts with low overall annual survival.
4. Population models projected that these impacts on annual juvenile survival substantially reduced population decline, such that population size at the end of the 8-year intervention was approximately double that without management.

5. *Synthesis and applications*. Our results show how complex patterns of within-year and among-year variation in exposure and efficacy of targeted conservation interventions can arise and scale up to affect population-level outcomes. We demonstrate overall positive effects of a joint supplementary feeding and parasite treatment intervention on the focal chough population, but also highlight potential routes to improve efficacy, for example, through more precise targeting of interventions and agricultural management actions in the context of among-year variation in environmental conditions.

**KEYWORDS**

annual juvenile survival probability, evidence-based conservation, multi-state mark-recapture, population growth rate, red-billed chough, seasonal demographic variation, supplementary feeding

## 1 | INTRODUCTION

Effective conservation of threatened populations requires identification and mitigation of key demographic constraints that limit population growth rate ($\lambda$), and requires thorough evaluation of management intervention efficacy (Hammers et al., 2015; Plard et al., 2020; Sarno et al., 1999; Sibly & Hone, 2002). However, identifying the causes and timing of demographic constraints, and implementing and evaluating targeted interventions, can be challenging. Not least, demographic constraints and magnitudes of responses to interventions could vary both within and among years, substantially affecting overall efficacy. Yet, such temporal variation, and its implications for optimal conservation management, are rarely explicitly quantified.

Despite increasing appreciation that vital rates commonly vary within years, and hence that constraints on $\lambda$ can be temporally restricted (Flockhart et al., 2015; Guimarães et al., 2020; Rushing et al., 2017; Sergio et al., 2019), individual- and population-level responses to anthropogenic change, including management impacts, are typically evaluated on overall annual timeframes (Marra et al., 2015). For example, threatened populations are commonly thought to be food-limited (e.g. Amar et al., 2005; Plard et al., 2020), but even when interventions aim to remedy perceived seasonal variation in natural food supply, outcomes are often evaluated solely at the annual scale (e.g. Siriwardena et al., 2007). However, within-year variation in vital rates and management impacts could limit overall efficacy (Timberlake et al., 2019). For example, if management aiming to sustain high annual survival successfully increases survival early in the annual biological cycle but fails in subsequent months, then overall objectives may not be met. Similarly, if substantial mortality occurs before management takes effect in the annual cycle, then annual survival will be relatively low even if subsequent management increases survival probability of remaining individuals. Moreover, if mortality is primarily concentrated within specific time periods, there may be little benefit in implementing year-round management. Such constraints may also vary among years. For example, when environmental conditions limit vital rates, management may be more effective when conditions are poor (Hammers et al., 2015; Timberlake et al., 2019). Explicitly quantifying both within-year and among-year variation in vital rates, and in management efficacy in ameliorating demographic constraints, is therefore necessary for designing optimally targeted and cost-effective interventions.

Juvenile survival (i.e. survival after fledging or weaning) is one vital rate that commonly varies substantially both within and among years, and can consequently drive variation in $\lambda$ (Gaillard et al., 2000; Koons et al., 2017; Reid et al., 2004; Wiens et al., 2006). Managing juvenile survival may therefore be important for conservation success (Ha et al., 2010; Manlik et al., 2016; Sarno et al., 1999). Yet, comparatively few conservation programmes explicitly target juvenile survival rather than other vital rates such as adult survival or breeding success (but see Ha et al., 2010; Zeoli et al., 2008). For example, supplementary feeding, a widely used conservation tool, is typically targeted at breeding adults and/or dependant young (e.g. González et al., 2006; Schoech et al., 2008). There are consequently few data on efficacy of supplementary feeding to increase juvenile survival, despite food limitation being a common constraint (e.g. Wiens et al., 2006).

Improved management consequently requires quantification of within-year and among-year variation in efficacy of targeted interventions in increasing juvenile survival. This is particularly challenging, especially when juveniles are mobile rather than territorial, and may move between unmanaged and managed areas at different times. Indeed, successful conservation will depend not only on the timing and magnitude of intervention impacts, but also on the proportion of individuals exposed to the intervention (Newey et al., 2010), which may vary temporally (Chamberlain et al., 2005). Juvenile movements may consequently underlie temporal variation in demographic constraints and management success. Quantifying how impacts of local conservation interventions scale up to affect realised population-wide survival probabilities is then not straightforward, but is critical to understand overall impacts on $\lambda$.

One population of immediate conservation concern, that is threatened by low juvenile survival and subject to a corresponding

targeted intervention, is the red-billed chough (*Pyrrhocorax pyrrhocorax*, hereafter 'chough') population inhabiting the island of Islay, Scotland (representing 87% of Scottish pairs in 2017). Islay's population decreased from ~95 to ~55 breeding pairs during 1986–2007, associated with agricultural change (Trask et al., 2020, Appendix S1). Analyses of long-term demographic data identified variation in juvenile survival as the main driver of population dynamics, which in turn was substantially explained by variation in food (tipulid larvae) abundance and weather (Reid et al., 2004, 2008). A substantial decrease in juvenile survival probability to ~0.1 in 2007–2009 (from ~0.42 pre-2007) then threatened population viability (projected $\lambda \approx 0.87$, Reid et al., 2011). This decrease resulted from low post-fledging survival in late-summer (July–September), attributed to low food availability (Reid et al., 2008, 2011, Appendix S1). Furthermore, post-mortem examinations revealed pathologically significant respiratory and alimentary tract parasite burdens, which may have exacerbated mortality (Trask et al., 2020; Appendix S1). Consequently, an emergency intervention comprising a targeted multi-year supplementary feeding programme (Bignal & Bignal, 2011), accompanied by antihelminthic treatment of visibly infected individuals (Trask et al., 2020), was enacted in key areas of Islay to try to prevent population extinction. To inform decisions to continue or refine this intervention, it is essential to quantify efficacy, and its variation within and among years, and hence evaluate overall population-level effects.

Such analyses must account for individuals' movements between managed and unmanaged areas within Islay and resulting temporal variation in management exposure, and account for imperfect detection of individuals across time. This can be achieved using multi-state mark–recapture models (White et al., 2006). Conceptually, such models consider that individuals can move between managed and unmanaged 'states' between discrete encounter occasions, and allow simultaneous estimation of exposure probabilities and exposure-dependent survival probabilities for successive time intervals within years. Overall annual-level effects can then be calculated.

Accordingly, we applied multi-state mark–recapture models to 8 years of intensive year-round resighting data from colour-ringed juvenile choughs to quantify variable juvenile exposure to management within and among years, and to estimate management efficacy in increasing within-year and annual juvenile survival. We then combined these estimates within matrix population projections to estimate overall impacts of the 8-year intervention on population size. We thereby provide the full, quantitative evaluation required to refine ongoing management.

## 2 | MATERIALS AND METHODS

### 2.1 | Management intervention and demographic monitoring

Supplementary feeding and parasite treatment protocols were designed to target juvenile choughs (Bignal & Bignal, 2011; Trask et al., 2020). Since juveniles typically move from natal territories to traditional communal foraging and roosting areas during the weeks following fledging (Figure 1a; Bignal et al., 1997), interventions were targeted in these communal areas (Appendix S1). In brief, supplementary food was provided near-daily during the non-breeding season (typically late-June to mid-April; Figure 1a; Bignal & Bignal, 2011) during eight annual biological cycles (2010–2011 to 2017–2018) within two broadly defined areas (termed feeding-area-1 and feeding-area-2, Appendix S1). Quantities of food (primarily mealworms and suet pellets with pinhead oatmeal) were limited, providing ~15% of individual daily energy requirements (Bignal & Bignal, 2011). During 2014–2018, some visibly infected individuals (signs of breathing difficulties, gaping with open bill, heading shaking, coughing) were caught at supplementary feeding sites and treated with antihelminthic ($n = 62$ individuals, Trask et al., 2020).

Each May–June during 2010–2017, almost all chough breeding territories on Islay were monitored, and samples of nestlings marked with unique colour-ring combinations ($n = 550$; $69 \pm 12$ *SD* nestlings/year, $24 \pm 4$ *SD* broods/year; ≥50% of nestlings fledged), allowing subsequent field identification of known individuals (following Reid et al., 2004, 2011; Appendix S1). Accordingly, the identities of colour-ringed individuals attending supplementary feeding were recorded throughout the year; near daily in feeding-area-1, and generally at least fortnightly in feeding-area-2. This generated high-quality, high-frequency data on individual attendance (totalling ~35,000 resightings of juveniles; full details of resighting regimes in Appendix S1). Extensive surveys were also undertaken across Islay, providing resightings of individuals that did not attend feeding areas (totalling ~2,600 resightings of juveniles). Additionally, intensive resighting surveys were undertaken each May during 2011–2018 (following Reid et al., 2011), resulting in very high annual resighting probability across all age classes ($P \geq 0.98$), allowing accurate direct calculation of overall first-year survival probability. As Islay's population is insular with no recent observations of permanent emigration, estimates of local 'apparent survival' represent true survival.

### 2.2 | Mark–recapture modelling approach

We used multi-state mark–recapture models to estimate transition probabilities ($\psi$) between 'states' that were or were not associated with the management intervention (see below), and estimate state-, time- (within-year) and cohort- (among-year) dependent survival probabilities ($S$) alongside temporally (within-year) and spatially varying detection probabilities ($p$).

Resightings were used to create state-specific individual encounter histories for all 550 individuals colour-ringed in eight annual cohorts fledged during 2010–2017. To provide the temporal resolution required to quantify within-year variation in survival and movement, especially during and around the previously identified survival bottleneck in July–September (observed in 2007–2009; Reid et al., 2011), histories were compiled across the annual biological cycle, from May in each individual's natal year (i.e. ringing) to May the following year. They comprised 10 defined encounter occasions

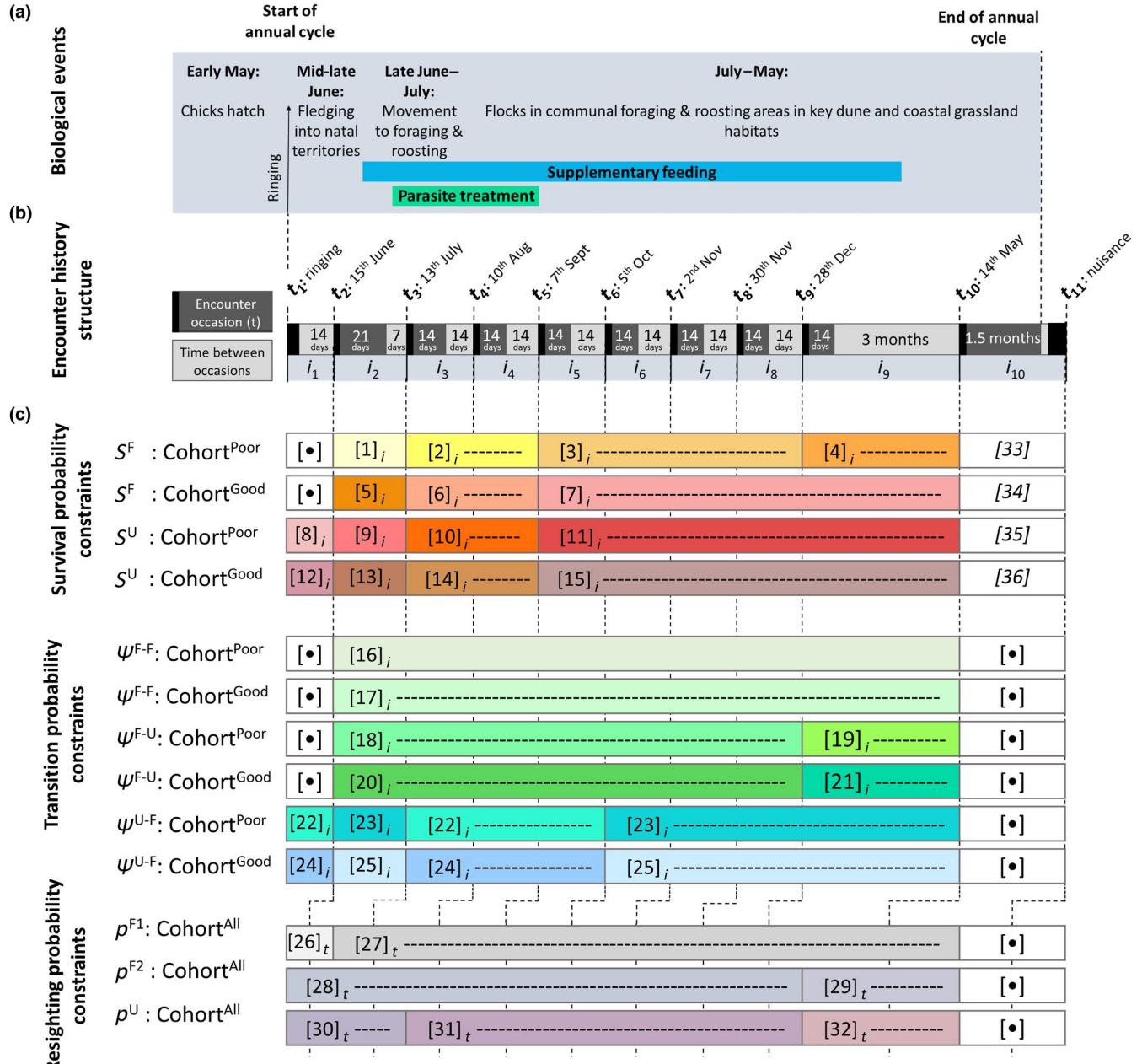


**FIGURE 1** Structure of multi-state mark–recapture models used to estimate within-year and among-year variation in exposure to management and associated variation in juvenile survival. (a) Summary timings of key biological and management events though an annual cycle. (b) Encounter history structure, comprising 11 encounter occasions ($t_1$–$t_{11}$), and 10 intervals ($i_1$–$i_{10}$) from colour-ringing in May. The final encounter occasion ($t_{11}$) is a nuisance parameter, describing whether an individual was observed after age one year; parameter estimates associated with $t_{11}$ and $i_{10}$ are not biologically meaningful. (c) Within-year constraints on group-dependent ('poor-survival' or 'good-survival' cohorts) and state-dependent (F = Fed, U = Unfed) survival ($S$), transition ($\psi$) and resighting ($p$) probability parameters in the 'Test Model' (full details, Appendix S3). The Test Model contained 36 parameters to be estimated, shown by numeric indices (32 biologically meaningful [$S$: [1]–[15], $\psi$: [16]–[25], $p$: [26]–[32]; 4 nuisance [*33*]–[*36*]), and highlighted by different colours. $S$ and $\psi$ parameters, and hence constraints, are associated with intervals ($i$), and $p$ parameters are associated with encounter occasions ($t$). Other parameter ([•]) values were fixed (Appendix S3). For example, since all individuals start in State-Unfed at ringing, there are no estimated State-Fed survival probabilities over $i_1$

($t_1$–$t_{10}$) at which $p$ was estimated, and hence nine intervals ($i_1$–$i_9$) over which $S$ and $\psi$ were estimated (Figure 1b). The first interval ($i_1$) corresponded to ringing to mid-June, followed by seven consecutive 4-week (i.e. 28 day) intervals from mid-June until the end of December ($i_2$–$i_8$; Figure 1b). To maximise use of resighting data, 21- or 14-day encounter occasions within each interval were defined (Figure 1b, Appendix S3). Since survival during January–May was previously relatively high (Reid et al., 2011), and because there were limited resightings away from supplementary feeding areas during this period, the final 15-week period ($i_9$) was defined as one interval (Figure 1b).

As $S$ and $p$ parameters for the final modelled interval and occasion may not be independently estimable from fully parameterised time-dependent models, an additional encounter occasion ($t_{11}$), and hence interval ($i_{10}$), was included, describing whether an individual was ever observed after age one year (Figure 1b). The resulting end $S$, $p$ and $\psi$ parameters are therefore nuisance parameters with no meaningful biological interpretation (estimates not reported), but mean that penultimate parameters that are of interest (for $t_{10}$ and $i_9$) are fully identifiable.

For each encounter occasion (excluding $t_1$), observed individuals were assigned to one of three mutually exclusive states based on their resighting location, and hence association with the intervention: at feeding-area-1 (hereafter 'State-Fed-1'), at feeding-area-2 (hereafter 'State-Fed-2') or elsewhere (hereafter 'State-Unfed'). Here, 'Fed' and 'Unfed' are used to reflect the observation circumstances. However, since parasite treatment was non-random with respect to apparent condition, state and year (only visibly ill individuals attending feeding sites in certain years were treated), effects of feeding and parasite treatment cannot be separated (Appendix S3). Survival probabilities associated with State-Fed consequently represent joint effects of both. All individuals were assigned to State-Unfed at $t_1$ (ringing). Consequently, there was no estimable survival probability for State-Fed-1 or State-Fed-2 over $i_1$ (Figure 1c, Appendix S3).

## 2.3 | Mark–recapture parameter constraints

As is inevitable for small populations of conservation concern, the small number of nestlings ringed each year (69 ± 12 *SD*, range: 56–94) precluded effective estimation of all $S$, $p$ and $\psi$ parameters in a fully time- (within-year), cohort- (among-years) and state-dependent model. Parameter structures were therefore necessarily constrained to facilitate estimation of key parameters regarding management efficacy. Constraints were designed to group parameters within and among years, and between states, based on knowledge of the system and field protocols, and thereby pragmatically balanced model complexity with biological realism (forming a 'Test Model', Figure 1c, Appendix S3).

First, the eight cohorts were divided into two 'cohort-groups' that coarsely captured previously known among-year variation in annual juvenile survival probability calculated from the May surveys (Appendix S1). These cohort-groups comprised six 'poor-survival' cohorts (2010, 2011 and 2014–2017) which had low annual survival probability (mean 0.19 ± 0.05 *SD*, $n$ = 420 individuals), and two 'good-survival' cohorts (2012 and 2013) which had higher annual survival probability (mean 0.38 ± 0.02 *SD*, $n$ = 130 individuals). This split allowed evaluation of among-group variation in management effects while minimising within-group heterogeneity that would violate key mark–recapture model assumptions. Creating two groups (rather than more) was the best feasible approach to capture among-year variation while allowing reasonable parameter estimation given available numbers of marked individuals and cohorts. This cohort-group structure was used for $S$ and $\psi$ parameters but not for $p$ (Figure 1c), since the consistent resighting efforts meant that state-dependent $p$ was unlikely to vary substantially among cohorts.

Second, corresponding $S$ and $\psi$ parameters for juveniles at the two feeding areas (State-Fed-1 and State-Fed-2) were constrained to be equal, thereby effectively representing a single overall 'State-Fed' (Figure 1c). This reduced model was much better supported than a model with separate State-Fed-1 and State-Fed-2 parameters (Appendix S3). However, full state dependence for $p$ was retained to capture known spatial variation in resighting effort (Appendices S1 and S3).

Third, within-year constraints on $\psi$ and $p$ parameters were set to capture known or postulated patterns of variation (Figure 1c; Appendix S3). Constraints on $\psi$ parameters distinguished transitions to and from feeding-areas post-fledging ($i_1$) and at the end of the annual cycle ($i_9$), and around previously identified periods of variable survival ($i_3$–$i_5$, Figure 1c). They also allowed estimation of $\psi$ between the two feeding-areas (i.e. between State-Fed-1 and State-Fed-2, Figure 1c; Appendix S3). Within-year constraints on $p$ captured known temporal variation in resighting effort (Figure 1c; Appendix S3).

Finally, within-year constraints on $S$ distinguished survival during the immediate-post fledging period ($i_1$) and in July–September ($i_3$ and $i_4$), from that during early summer ($i_2$) and late-autumn and winter ($i_5$–$i_9$, Figure 1c). The resulting Test Model contained 36 parameters to be estimated (32 biologically meaningful, 4 nuisance, Figure 1c).

## 2.4 | Mark–recapture model analyses

The Test Model was used to test hypotheses regarding impacts of management on occasion-dependent survival probability for each state (Appendices S2 and S3). Specifically, a series of candidate nested models, where parameters of interest were constrained to be equal (e.g. $S$ for State-Fed and State-Unfed for the same interval), were fitted and compared to the Test Model.

Models were fitted using program MARK (White & Burnham, 1999), adjusting survival estimates for uneven time intervals, and using Newton–Raphson optimization. The Test Model showed little overdispersion, and hence little evidence of major lack of fit (median variance inflation factor $\hat{c}$ ± *SE*: 1.17 ± 0.01, Appendix S3). There was no evidence of multiple maxima produced in the likelihood function (Appendix S3), implying that estimates represent the global maximum of the likelihood.

Akaike's information criterion, corrected for small sample size and overdispersion (QAICc), was used to assess relative support (Burnham & Anderson, 2002). Nested models were considered better and less well supported than the Test Model, implying that focal constrained parameters did not differ, if $\Delta$QAICc < −2. Alternatively, nested models were considered less well supported, implying that focal constrained parameters differed, if $\Delta$QAIC > +2. Full details of parameter estimates and model comparisons are in Appendix S3.

### 2.5 | Population-level effects

To quantify overall impacts of the intervention on population-wide annual juvenile survival (incorporating both exposure and exposure-dependent survival; Appendix S2), state-dependent $S$ estimates were weighted by the estimated proportions of individuals alive in State-Fed versus State-Unfed at each occasion. These proportions were estimated by calculating the probabilities of all 1,023 possible pathways of exposure and survival through the full annual cycle given state, within-year and among-year dependent $S$ and $\psi$ estimates from the Test Model and associated error (Appendix S4). Overall population-level 'realised' survival probabilities were then estimated as the sum of the products of all path probabilities at each occasion (Appendix S4).

These 'realised' values were compared to a hypothetical 'worst-case' scenario with no management, and a hypothetical 'best-case' scenario where all individuals experienced management throughout the annual cycle. These two scenarios were respectively parameterised by considering that all surviving individuals at $t_2$ either remained in State-Unfed, or transitioned to and remained in State-Fed. To generate survival probabilities for both scenarios, sequential estimates of $S$ were multiplied to generate monthly and annual survival estimates for 'poor-survival' and 'good-survival' cohorts separately. Approximate 95% confidence intervals (95% CIs; i.e. 2.5th–97.5th percentiles) for realised and hypothetical scenarios were calculated by sampling 10,000 times from normal distributions of $S$ approximating estimates and 95% CIs from the Test Model (Appendix S5).

To explicitly estimate how intervention effects on juvenile survival alone affected population size over the intervention period (2010–2017), we used pre-breeding census, birth-pulse, stage-structured Lefkovitch matrix multiplications (Appendix S5). Three models were parameterised using annual juvenile survival probability estimates from the three modelled scenarios ('realised', 'worst-case' and 'best-case'), accounting for the observed sequence of 'poor-survival' and 'good-survival' cohorts. Given the objective of evaluating population-level consequences of management on juvenile survival, all other vital rates were set to constant baseline values (Appendix S5). Associated 95% CIs were calculated as above, using distributions of estimated annual juvenile survival.

## 3 | RESULTS

### 3.1 | Resighting and transition probabilities

Estimates of $p$ varied within years and among states, reflecting known variation in resighting effort (Figure 2a; Appendix S3). Values were always high for State-Fed-1, and for the May survey ($t_{10}$, Figure 2a), generating sufficient power to estimate $S$ and $\psi$ parameters of interest.

Estimates of $\psi$ from State-Unfed to State-Fed were high across the annual cycle, particularly in 'good-survival' cohorts (Figure 2b,c). In contrast, $\psi$ from State-Fed to State-Unfed was generally low, as was $\psi$ between the two Fed states (Figure 2b,c). Consequently, a high proportion (>70%) of surviving ringed juveniles were exposed to management at each occasion (Figure 3a,b). Only in the final occasion in 'good-survival' cohorts (Figure 3b) was a majority of surviving individuals in State-Unfed because of high $\psi$ from State-Fed to State-Unfed in $i_9$ (Figure 2c).

### 3.2 | Survival probabilities

During the first interval after ringing ($i_1$), $S$ was similar in 'poor-survival' and 'good-survival' cohorts (Figure 2d,e; nested model better supported, ΔQAICc = −2.0, Appendix S3). Furthermore, survival during $i_2$ did not differ between State-Fed and State-Unfed for either 'poor-survival' cohorts (ΔQAICc = −1.1) or 'good-survival' cohorts (ΔQAICc = −1.5). However, $S$ differed between State-Fed and State-Unfed through subsequent intervals, and furthermore, these differences differed between 'poor-survival' and 'good-survival' cohorts (Figure 2d,e).

For 'poor-survival' cohorts, $S$ was low during $i_3$–$i_4$ (July–September) for both State-Fed and State-Unfed (Figure 2d), but was marginally higher for State-Fed (ΔQAICc = +1.5). $S$ was then higher for State-Fed across intervals $i_5$–$i_9$ (September–May) compared to $i_3$–$i_4$ (ΔQAICc = +13.8), but remained similar for State-Unfed (ΔQAICc = −2.0, Figure 2d). Consequently, $S$ during $i_5$–$i_9$ was considerably higher for State-Fed than for State-Unfed (ΔQAICc = +11.3). The low estimates of $S$ for State-Unfed resulted in very low time-adjusted survival through the long interval between December and May ($i_9$).

In contrast, for 'good-survival' cohorts, there was little difference in $S$ between State-Fed and State-Unfed (Figure 2e). Survival was similar in both states during $i_3$–$i_4$ (ΔQAICc = −2.0), and during $i_5$–$i_9$ (ΔQAICc = −1.9). However, $S$ for State-Fed was still lower during $i_3$–$i_4$ than during $i_5$–$i_9$ (ΔQAICc = +3.8), while $S$ for State-Unfed did not differ across these two periods (ΔQAICc = −1.5). This is because estimates for State-Unfed were very imprecise (Figure 2e), which is inevitable because high $\psi$ to State-Fed in 'good-survival' years (Figure 2c) left few individuals in State-Unfed.

### 3.3 | Population-level effects

Due to high $\psi$ from State-Unfed to State-Fed and low $\psi$ from State-Fed to State-Unfed (Figure 2b,c), and generally high $S$ for State-Fed (Figure 2d,e), most surviving individuals at each occasion were in State-Fed, particularly in 'good-survival' cohorts (Figure 3a,b). In 'poor-survival' cohorts, the estimated 'realised' annual survival probability, which incorporated surviving individuals in both states at each occasion, was substantially greater than both the 'worst-case' scenario ($\Phi$ = 0.16, 95% CI 0.13–0.20 vs. 0.02, 95% CI 0.01–0.04, Figure 3c asterisks), and the low survival observed during 2007–2009 ($\Phi$ = 0.10, Reid et al., 2011) which prompted the management intervention. 'Realised' survival was, however, substantially lower

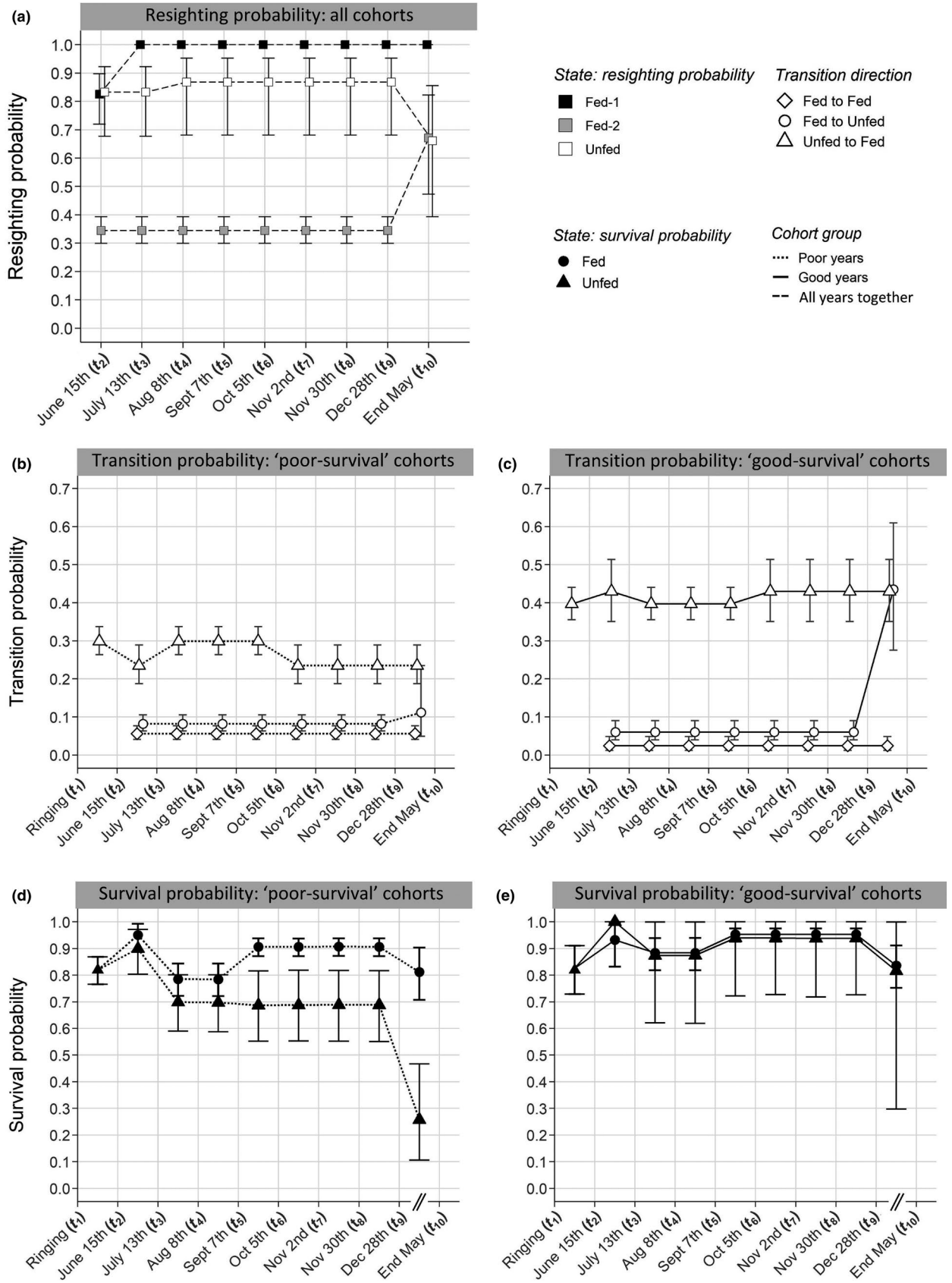


**FIGURE 2** Test Model parameter estimates with 95% confidence intervals. (a) State and time (within-year) dependent resighting probabilities. State, time and cohort (among-year) dependent (b&c) transition and (d&e) survival probabilities in 'poor-survival' (b&d) and 'good-survival' (c&e) cohorts. *X*-axis labels indicate the start date of each encounter occasion or interval. Points (jittered to aid visualisation) show transition or survival probabilities across corresponding intervals. The lower survival probability during January–May reflects the long interval

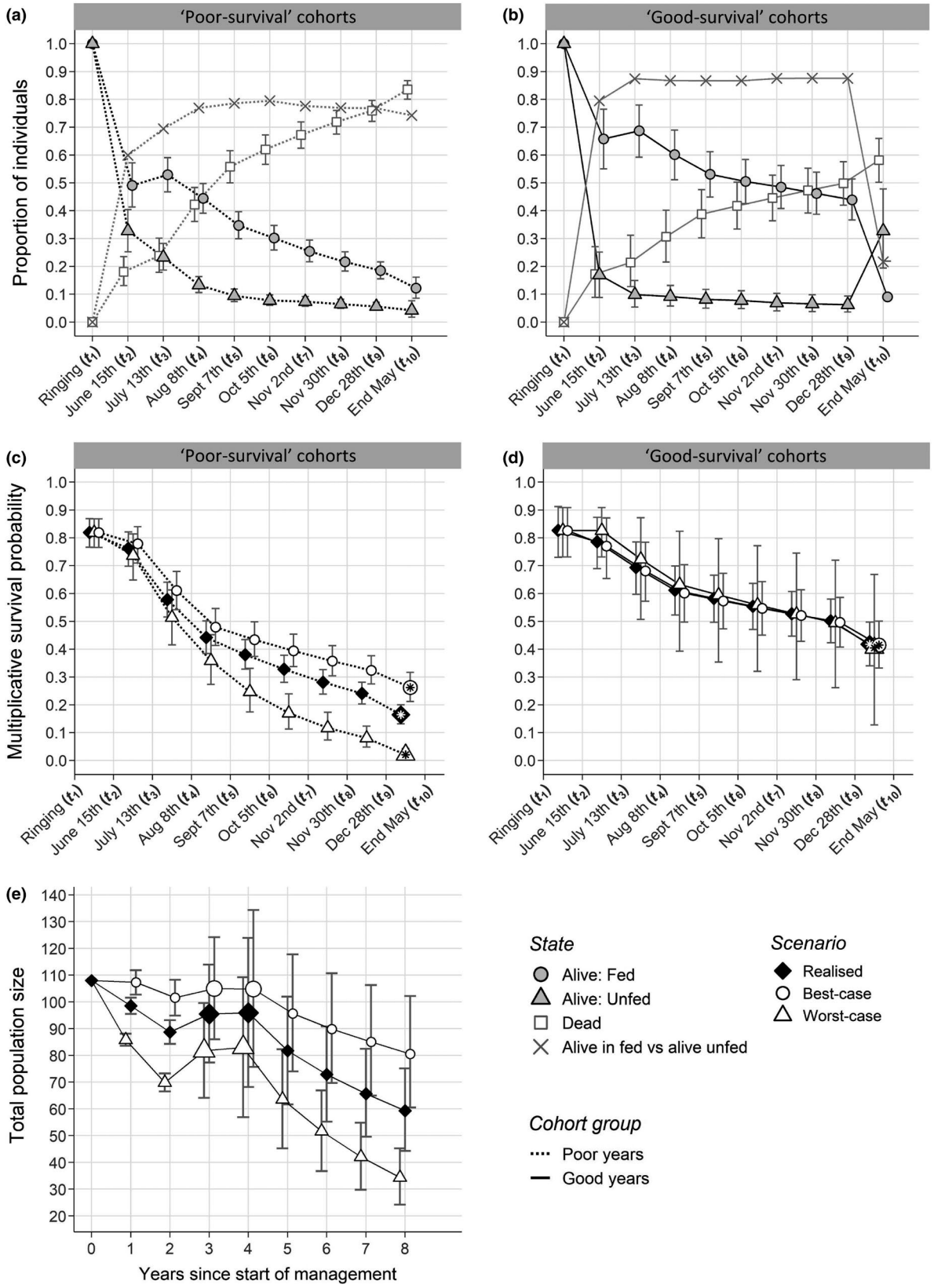


**FIGURE 3** Derived estimates (with 95% confidence intervals) of management impacts from the Test Model. Time (within-year) and cohort (among-year) dependent proportion of individuals alive in State-Fed, alive in State-Unfed, dead or alive in fed versus alive in unfed in (a) 'poor-survival' and (b) 'good-survival' cohorts. Multiplicative 'realised' survival probabilities compared to hypothetical 'worst-case' and 'best-case' scenarios for (c) 'poor-survival' and (d) 'good-survival' cohorts (annual-level probabilities highlighted by final points with asterisks). (e) Estimated total population sizes across the intervention period (2010–2018) for each scenario (small and large points show 'poor-survival' and 'good-survival' cohorts, respectively). Points are jittered to aid visualisation

than the 'best-case' scenario ($\Phi = 0.26$, 95% CI 0.21–0.32, Figure 3c asterisks). In 'good-survival' cohorts, there was no difference between 'realised', 'worst-case' and 'best-case' scenario annual survival estimates ($\Phi = 0.42$, 95% CI 0.34–0.50; $\Phi = 0.40$, 95% CI 0.13–0.67 and $\Phi = 0.41$, 95% CI 0.33–0.50, respectively), although the 'worst-case' estimates were again imprecise (Figure 3d).

Due to the positive estimated intervention effects in the 'poor-survival' cohorts (i.e. in 6 of 8 years), the matrix models estimated that the intervention substantially reduced the decrease in population size that was otherwise projected to have occurred. Population size at the end of the 8-year period was predicted to be approximately double that without management (Figure 3e).

## 4 | DISCUSSION

Quantifying within-year and among-year variation in exposure to management interventions in mobile individuals, and quantifying associated variation in exposure-dependent survival probabilities and resulting population-level impacts, is necessary to design efficient and effective management strategies. However, this is highly challenging. Our multi-state analyses of unusually high-frequency resighting data from a threatened chough population show that substantial proportions of ringed juveniles were exposed to an intervention, comprising supplementary feeding and targeted parasite treatment, during the annual cycle. Estimated survival probabilities were higher for exposed versus unexposed individuals, but only during certain periods within years, and in certain years. These estimated effects were sufficient to slow the rapid projected population decline, but also reveal potential routes to refine future management.

Since food limitation is likely to constrain survival probabilities and $\lambda$ of many threatened populations, supplementary feeding is a common intervention. Yet, while some studies have quantified individual (Crates et al., 2016; Maggs et al., 2019) and spatial (González et al., 2006) variation in supplementary food use, temporal variation in exposure is rarely quantified or incorporated into assessments of overall management impacts. Our analyses show high uptake of management throughout the annual cycle, highlighting the value of prior knowledge of a population's natural behaviour and ecology in facilitating targeted interventions. Given such high exposure, any increase in survival probability associated with the intervention could increase population-wide survival probability and hence population size.

In practice, realised population-level impacts of supplementary feeding programmes are infrequently explicitly quantified (Ewen et al., 2015; Martínez-Abraín & Oro, 2013), hindering evidence-based refinement. Our analyses show that, in years of lower overall annual survival ('poor-survival' cohorts), survival probabilities early in the annual cycle (July–September) were somewhat higher for individuals that experienced management than those that did not, and were substantially higher through the subsequent winter–spring (January–May). Low chough survival probabilities during July–September were previously linked to low natural food availability, both on Islay (Reid et al., 2011) and Ouessant, France (Kerbiriou & Julliard, 2007). Furthermore, among-year variation in annual juvenile survival probability was previously tightly associated with winter tipulid larvae abundance (Reid et al., 2008), implying that winter survival is also food-limited. Estimated increases in survival probability in State-Fed may therefore directly reflect reduced starvation and/or parasite loads due to the interventions. Alternatively, increases may arise through compound effects if feeding increases individual condition sufficiently to improve parasite tolerance, and/or reduces consumption of natural 'fallback' prey with higher parasite transmission risk.

However, during 2 years of higher observed annual survival ('good-survival' cohorts), there was no evident difference in survival probability between defined Fed and Unfed states, and hence no apparent effect of the intervention on juvenile survival. Studies on other systems concluded that, as generally makes intuitive sense, supplementary feeding may have less impact during periods of high natural food availability, when survival is not food-limited (Ruffino et al., 2014; Sim et al., 2015). However, there are rarely data on natural food availability to investigate this possibility. In our system, the two 'good-survival' cohorts coincided with years of very high winter (post-fledging) tipulid larvae abundance, compared to the six 'poor-survival' cohorts (means $2{,}215 \times 10^3 \pm 463 \times 103$ *SD* and $876 \times 10^3 \pm 442 \times 10^3$ *SD* tipulids $ha^{-1}$ $year^{-1}$, respectively, Appendix S3). The apparent lack of intervention impacts for 'good-survival' cohorts may therefore partly reflect better environmental conditions, resulting in high estimated winter survival for individuals in State-Unfed. While winter tipulid abundance cannot directly explain the lack of difference in survival between State-Fed and State-Unfed in July–September, it may indicate some form of correlated environmental conditions, such as availability of other invertebrate prey, or beneficial weather (Reid et al., 2008).

However, since transition probabilities to State-Fed were higher in 'good-survival' cohorts than 'poor-survival' cohorts, more individuals were exposed to the intervention and very few individuals remained in State-Unfed. The higher annual survival probability may therefore partly reflect these cohorts' higher exposure to the intervention. The interannual (i.e. between cohort-groups) differences in transition probabilities could themselves reflect differences in environmental conditions and/or associated social behaviour, but may mean that intervention impacts on survival probabilities in 'good-survival' cohorts are undetectable because so few individuals were in State-Unfed. Indeed, survival probabilities for State-Unfed were estimated imprecisely, meaning that potential positive (or negative) intervention effects cannot be definitively excluded. Nevertheless, since estimated survival probabilities for the two states were near identical, the conclusion that they did not differ does not necessarily reflect low power. There was consequently no conclusive evidence that the observed increased exposure for 'good-survival' cohorts was solely responsible for their higher annual survival probabilities.

Overall, our estimation that the targeted intervention increased juvenile survival, primarily in years with low winter abundance of a key prey, supports the original inference that juvenile chough

survival is food-limited (whether directly and/or indirectly through associated parasite exposure and social interactions). However, since the interventions were implemented as emergency responses rather than controlled randomised experiments, exact estimated effects, and inferences on underlying causes of variation, should be taken with appropriate caution. Our analyses cannot account for potential intrinsic differences between individuals that did and did not attend feeding areas at specific occasions. However, feeding took place at three separate locations (Appendix S1), and attendance was not strongly structured in relation to individuals' natal locations. The apparent positive effect observed in the 'poor-survival' cohorts is perhaps intuitively unlikely to simply reflect quality, since individuals with higher mortality risk might be expected to use the supplementary food most. If that were true, our analyses could underestimate positive intervention effects. Nevertheless, at face value, our estimates suggest that the intervention effects on juvenile survival were sufficient to reduce (but not prevent) population decrease. Previous analyses showed that the intervention also had substantial collateral benefits, by increasing adult survival probability and components of reproductive success (Fenn et al., 2020). Together, these results imply that the intervention successfully prevented a rapid population decline (Trask et al., 2019). Indeed, observed population size has been approximately stable since 2014.

### 4.1 | Management implications and context

Proactive conservation should ideally iterate through cycles of evidence-based design, implementation and (re-)evaluation of targeted interventions (Sutherland et al., 2004), yet comparatively few conservation-focused studies evaluate intervention efficacy (Williams et al., 2020). Studies that do not evaluate variation in responses among seasons or years also risk providing misleading assessments. Our results suggest that responses to targeted supplementary feeding and parasite treatments are temporally variable, opening potential routes to further increase efficacy and cost-effectiveness. For example, the remaining period of low survival during July–September could potentially be further ameliorated by providing more food during this relatively short period, and/or implementing parasite treatments sooner after fledging. Since management had little detectable effect in some years, cost-effectiveness could in principle be improved by evaluating survival rates in autumn each year, and inferring whether food provisioning is warranted throughout the winter and spring. Furthermore, since not all juveniles experienced management, overall efficacy could potentially be increased through additional feeding sites. The current implementation was facilitated by chough social behaviour, whereby most sub-adults congregate in relatively discrete areas. Monitoring during the supplementary feeding programme has further increased understanding of post-fledging behaviour, which may help identify additional sites for future targeted feeding, although wider implementation may prove logistically difficult.

Nevertheless, while intensive conservation interventions are often required to slow or prevent extinction of threatened populations (e.g. Oro et al., 2008), they are not necessarily sustainable or desirable long term. Supplementary feeding, and associated parasite treatments, should ideally only be enacted until habitat management to increase safe natural food resources is in place (Schoech et al., 2008). Long-term persistence of Scottish choughs will require targeted management initiatives that increase the availability, abundance, and spatial and temporal diversity of natural food in traditional chough foraging areas, particularly in key grassland and sand dune systems within nursery areas (Trask et al., 2020). Consequently, in common with other grassland bird species, effective, long-term conservation will ultimately rely on appropriate and effective land management programmes.

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## CONFLICT OF INTEREST

The authors have declared no conflict of interest.

## AUTHORS' CONTRIBUTIONS

All authors contributed to conceptual development. S.R.F. and J.M.R. devised the analyses; S.R.F. undertook the analyses; E.M.B. and S.B. managed and undertook supplementary feeding and data collection, with contributions from D.I.M., J.M.R., A.E.T. and S.R.F.; S.R.F. wrote the manuscript with contributions from J.M.R., with input and final approval from all authors.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.g1jwstqrh (Fenn et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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